4 | Early Land Floras

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Abstract: The main objects of this review are to give some idea of the general appearance, habit and affinities of early vascular plants and to present the meagre evidence pertinent to the reconstruction of terrestrial vegetation in late Silurian and Devonian times. The description of vascular plants in the late Silurian (Ludlow Series) provides unequivocal evidence for the existence of terrestrial vegetation. By early Pridoli, floras of remarkable uniform composition were widespread. These comprised plants showing great simplicity of organization with a predominance of rhyniophytes and centred on the genus *Cooksonia*. Later Gedinnian floras indicate the beginnings of diversification with the appearance of zosterophyllophytes, but it is in the later Lower Devonian that extensive assemblages of very varied composition are first recorded. These include the first lycopods as well as the trimerophytes, which are considered intermediate in organization between the earliest vascular plants and the Middle Devonian ferns, "pre-sphenopsids" and progymnosperms. Although recent anatomical and morphological studies on Silurian and Devonian macroplants have permitted such an evolutionary overview and have resulted in major revisions of their classification, it is concluded that little progress has been made in elucidating details of terrestrial vegetation.

INTRODUCTION

The two recent major reviews of Devonian floras by Chaloner and Sheerin (1979) and by Banks (1980b) more than adequately reflect the intensity of interest and activity in the study of early land plants. Banks' attempt at a stratigraphy of late Silurian (Pridoli) and Devonian sediments based on macroplants, in which he distinguishes seven generic assemblage zones, is the outcome of the

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accumulation of a wealth of data, both morphological and anatomical, over the past 60 years. Such data have also made possible important revisions in the classification of early vascular plants: the "psilophytes", for example, have been replaced by three new subdivisions, Rhyniophytina, Zosterophyllophytina and Trimerophytina (Banks, 1968a, 1975a), and Beck (1960) established a new class, the Progymnospermopsida, comprising plants with pteridophyte reproduction and gymnospermous anatomy. Both of the recent reviews emphasize the late Silurian and Devonian as a period of major evolutionary innovation, a time of diversification following the initial colonization of the land.

In general appearance, this early terrestrial vegetation would be strikingly different from that of the present day which is dominated by a wide variety of different forms of leaf. Apart from lycopods and more enigmatic plants with fan-shaped leaves, plants consisted of collections of stem-like structures, variously branched. Thus, instead of presenting yet another review of early land floras, I propose to illustrate some of the commonest genera to give some idea of the appearance of individual plants. Although it would be highly desirable to be able to group these plants into communities and then to speculate on their palaeoecology, there is unfortunately less direct evidence for the reconstruction of vegetation in the Siluro-Devonian than at any other time in the history of plant life on land.

Exactly when plants first colonized land surfaces remains a matter of considerable conjecture (e.g. Banks, 1972, 1975b,c; Gray and Boucot,1977; Edwards *et al.*, 1979). In this account I shall concentrate on vascular plants, which, as Raven (1977) in his novel physiological approach to the early evolution of vascular plants has pointed out, are able to regulate their rate of water loss because they possess a gas-impermeable cuticle and functional stomata connected to an intercellular space system. They thus remain hydrated even when their water supply is limited. Such homoiohydric plants are the true conquerors of the land and such a level of anatomical organization is seen in the probably mid-Siegenian Rhynie Chert plants (Kidston and Lang, 1917. Earlier coalified compression fossils of vascular plants lack the superb cellular preservation found in the Chert and so it is impossible to determine whether or not plants such as *Cooksonia* had attained this degree of water control. Nevertheless the demonstration of vascularized axes and fertile plants assignable to *Cooksonia* in the Ludlow Series of south Wales (Edwards and Davies, 1976; Edwards and Rogerson, 1979; Edwards *et al.*, 1979) is a firm indication that plant life existed on land in the late Silurian.

Some workers (e.g. Gray and Boucot, 1977; Pratt *et al.*, 1978) have argued very forcefully that pre-Ludlow microfossil evidence indicates the presence of terrestrial vegetation prior to the appearance of vascular plant macrofossils, although the affinities of these plants remain obscure. Such microfossils include resistant spores with triradiate marks (Gray and Boucot, 1971, 1974), cuticle-like films bearing the outlines of cells, sheets of cells and tubes with thickenings paralleling those seen in tracheids (Pratt *et al.*, 1978).

Fragments of similar type are found in the same sediments as early vascular plants (see, for example, Lang, 1937) as indeed are non-vascular plant macrofossils such as *Parka*, *Pachytheca* and *Prototaxites*. Whether or not these grew on the surface of the ground or were immersed in fresh water cannot be determined with certainty. Niklas (1976a) has compared the organization of *Parka* with that of an extant green alga *Coleochaete*: affinities with the Chlorophyta being further supported by chemical analysis (Niklas, 1976b). The presence of a thin, cuticle-like covering led Niklas to suggest that *Parka* grew as an epiphyte in shallow freshwater pools, subject to periods of desiccation. The affinities of *Pachytheca* have been considered with the blue-green (Lang, 1945) and green algae (Niklas, 1976b). Indeed Niklas suggests the possibility that *Parka* and *Pachytheca* were related on the basis of similar patterns of growth as well as chemical analyses. *Prototaxites* is also difficult to assign to an extant algal group, although often considered to be brown (Johnson and Konishi, 1958; Schmid, 1976). Niklas (1976c) has isolated cutin and suberin derivatives from coalified compressions which indicate that *Prototaxites* too could have survived on land. Indeed if *Prototaxites* was similar to extant algae in lacking an intercellular space system, it is difficult to understand how, with a trunk 1 m in diameter and more than 2 m long (records from the Lower Devonian of Canada–Schmid, 1976), it could have survived completely immersed in water without the central region becoming anaerobic (Raven, 1977 and personal communication).

SILURIAN PLANTS

1. Assemblage Zone I : Cooksonia *(mid-Ludlow to end of Pridoli; Fig. 1)*

Following the recent discovery of *Cooksonia* Lang in Bringewoodian strata in central Wales (*incipiens* Zone; Ludlow Series) Banks' Assemblage Zone I is extended back to mid-Ludlow sediments. Although there are reports of pre-Pridoli vascular plants from Libya (Boureau *et al.*, 1978) and Australia (Garratt, 1979), it is only in Wales that macrofossils of vascular plant aspect occur in sediments in which the stratigraphical dating is supported unequivocally by independent

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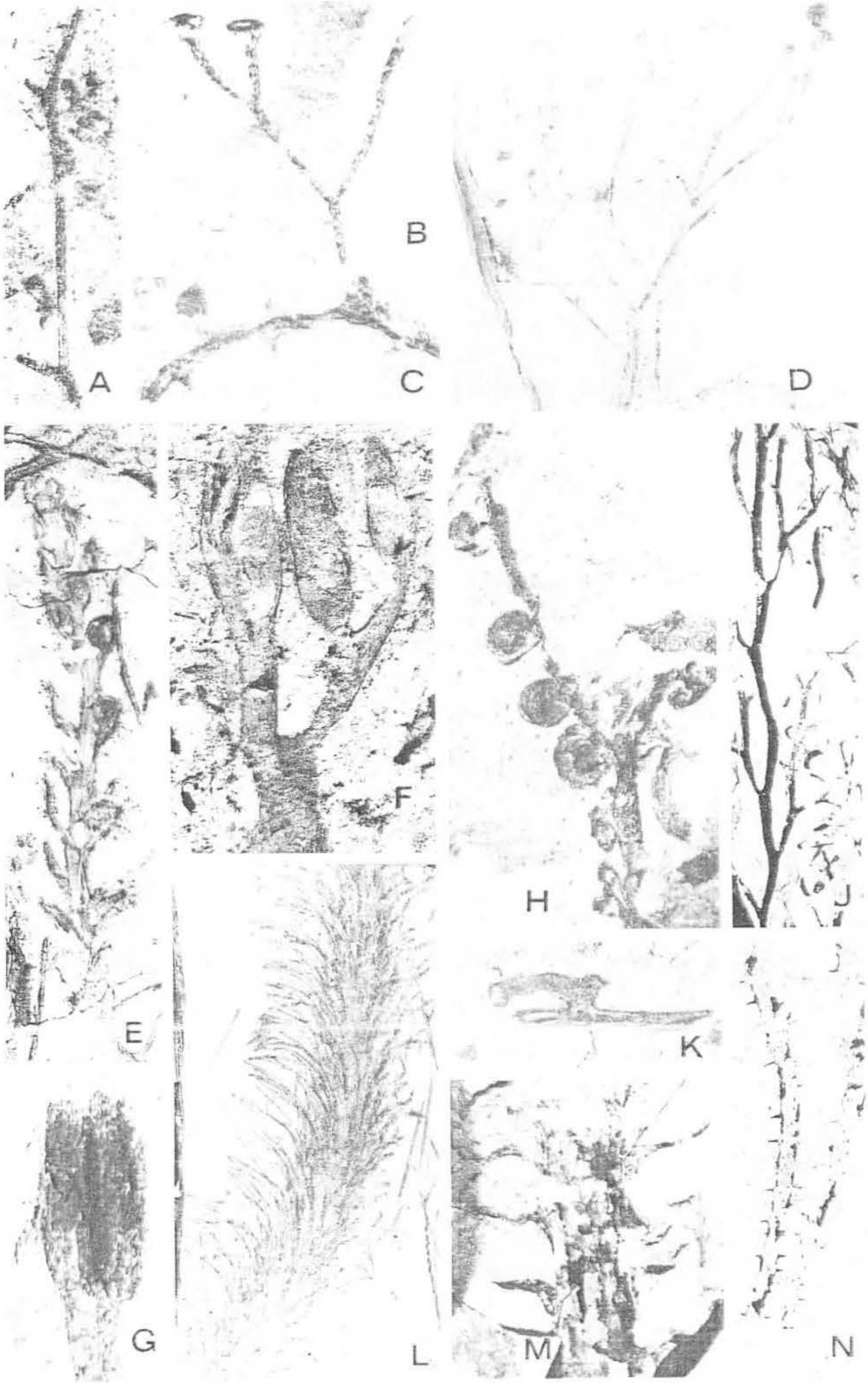
Fig. 1. (opposite). Silurian plants A–D: (A) *Hostinella* Stur – smooth dichotomously branching axis; *incipiens* Zone (Ludlow Series), Wales (× 3·2). (B) *Cooksonia pertoni* Lang – smooth forking axis terminating in oval sporangia; *incipiens* Zone (Ludlow Series), Wales (× 3·1). (C) *Psilophytites* Høeg – axis with triangular spines (enations); Pridoli (Downton), Wales (× 8). (D) *Steganotheca striata* Edwards – smooth dichotomously branching axes with elongate terminal sporangia; Pridoli (Downton), Wales (× 1·2).

Devonian plants E–N: (E) *Zosterophyllum myretonianum* Penhallow – spike of spirally inserted lateral sporangia; ?early Siegenian (Dittonian), Scotland (× 1·2). (F) *Hedeia corymbosa* Cookson – cluster of elongate sporangia terminating smooth axes; ?Siegenian–Emsian, Australia (× 3·3). (G) *Yarravia oblonga* Lang and Cookson – cluster of elongate sporangia fused in basal region; ?Siegenian–Emsian, Australia (× 3·7). (H) *Gosslingia breconensis* Heard – smooth axes with scattered reniform, lateral sporangia; Siegenian, Wales (× 4·2). (J) *Gosslingia breconensis* Heard – sterile branching specimen showing pseudomonopodial branching; Siegenian, Wales (× 0·6). (K) *Zosterophyllum australianum* Lang and Cookson – sterile smooth branching axis showing K-configuration; ?Siegenian–Emsian, Australia (× 2·3). (L) *Baragwanathia longifolia* Lang and Cookson – stem covered with elongate narrow leaves (microphylls); ?Siegenian-Emsian, Australia (× 0·4). (M) *Drepanophycus spinaeformis* Goeppert – stem with falcate leaves (microphylls); Emsian, Gaspé, Canada (× 0·7). (N) *Sawdonia ornata* Hueber – sterile axis with pointed spines; Emsian, Canada (× 0·8).

(A,B) from Edwards *et al.*, 1979; (C) from Edwards, 1979; (D) from Edwards, 1970a; (E) from Edwards, 1975; (F,K) from Cookson, 1935; (G) from Lang and Cookson, 1935; (H,J) from Edwards, 1970b; (K,L) from negative loaned by J. Tims; (M) from Stubblefield and Banks, 1978; (N) from collection of author.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faunal content (Banks, 1980b; Chaloner and Sheerin, 1979; Edwards *et al.*, 1979).

By early Pridoli times, *Cooksonia* dominated floras were widespread, occurring in Bohemia (Obrhel, 1962), New York State (Banks, 1973), the U.S.S.R. (Ischenko, 1975), southern Britain (Lang, 1937; Edwards, 1979; Edwards and Rogerson, 1979) and possibly north Africa (Daber, 1971). *Cooksonia* itself (Fig. 1B) was a small plant, not more than a few centimetres high, consisting of a tuft of smooth, forking axes which terminated in spherical or ellipsoidal sporangia. It is known only from the compression fossils. *Steganotheca* (Fig. 1D) looks very similar but has elongate sporangia, each with a lens-shaped apical thickening (Edwards, 1970a; Edwards and Rogerson, 1979). By far the commonest vascular plant fossils in these Ludlow–Pridoli sediments are smooth, dichotomously branching sterile axes (Fig. 1A) which are placed in the form genus, *Hostinella* (Banks, 1968b). In addition, Obrhel records unbranched axes with a narrow central line as ?*Taeniocrada*, while in an extensive flora from south Wales (Edwards, 1979) I have described axes with spines (Fig. 1C) as well as smoother axes with more complex branching.

DEVONIAN PLANTS

1. *Assemblage Zone II :* Zosterophyllum *(Gedinnian to mid-Siegenian; Fig. 1)*

This zone is marked by the appearance of a second type of vascular plant organization. In *Zosterophyllum* (Fig. 1E) sporangia are borne laterally on smooth axes and are aggregated into terminal spikes (Lang, 1927). Dichotomous branching is still seen, but *Zosterophyllum* also has branches resembling the letters K and H (Fig. 1K). These are concentrated near the base of the plant so that it has a tufted appearance (Walton, 1964). If Richardson is correct in assigning, on palynological evidence, an early Siegenian age to the Scottish Dittonian floras (Westoll, in House *et al.*, 1977; Edwards, 1980) the oldest fertile *Zosterophyllum* is late Gedinnian or early Siegenian (Scotland – Lang, 1927; Belgium – Leclercq, 1942; Welsh Borderland – Edwards and Richardson, 1974). *Cooksonia* is recorded from the Gedinnian of Czechoslovakia (Obrhel, 1968) and the Dittonian of Scotland (Edwards, 1970a).

2. *Assemblage Zone III* : Psilophyton *(mid-Siegenian to end of Emsian; Figs 1 and 2)*

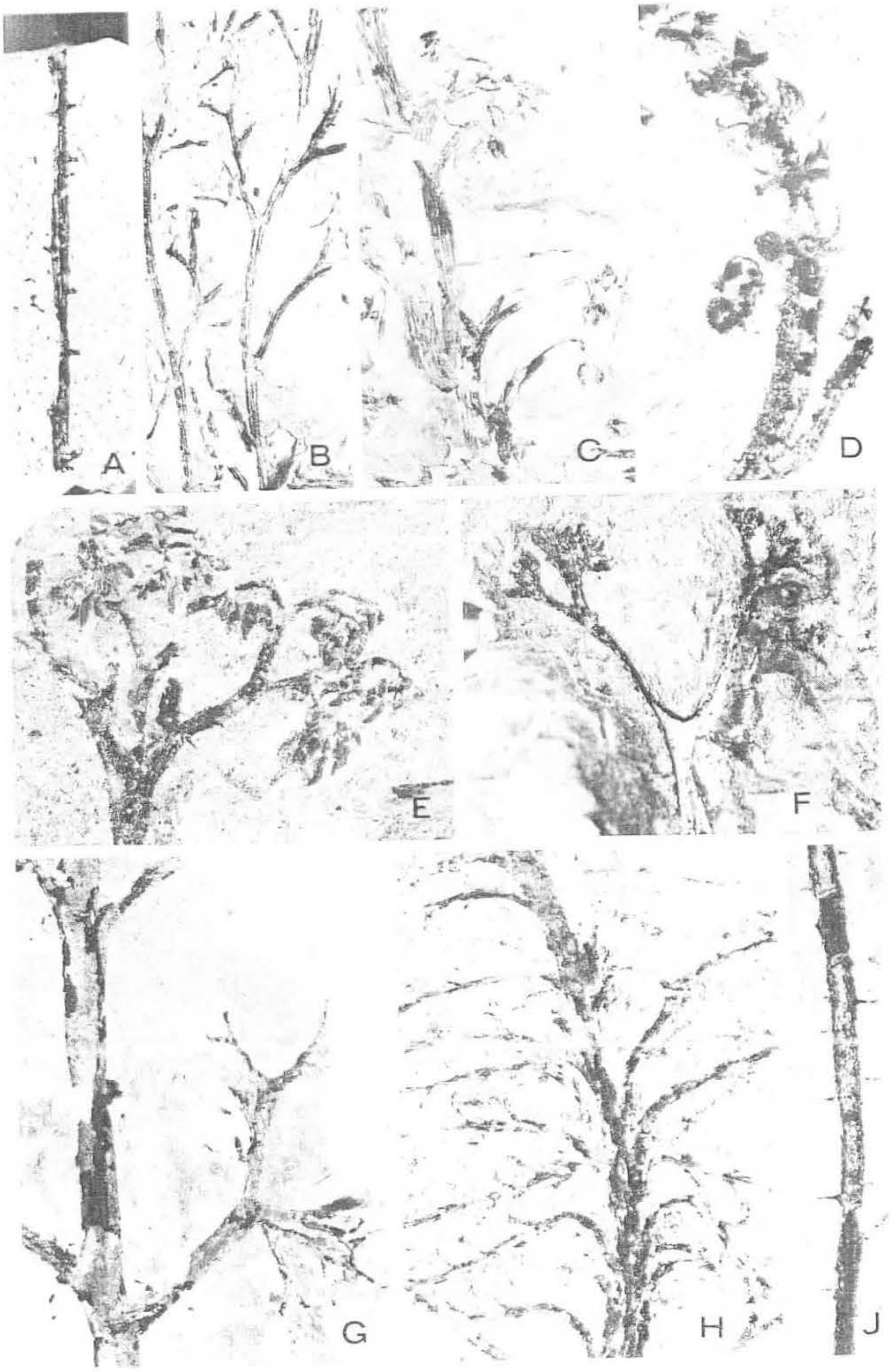
This zone has a much larger number of records of vascular plant assemblages, which show an overall increase in number of taxa and a greater diversity of forms. The discovery and description of various kinds of petrifaction (e.g. silica–Kidston and Lang, 1917; calcium carbonate–Banks *et al.*, 1975; iron sulphide–Edwards, 1970b) have yielded important information on three-dimensional anatomy.

Cooksonia is still represented in these floras (Croft and Lang, 1942), but far more complex rhyniophytes had already evolved. These include *Rhynia* and *Horneophyton* (Kidston and Lang, 1917) from the ?mid-Siegenian Rhynie Chert and *Yarravia* (Fig. 1G) and *Hedeia* (Fig. 1F) which have terminal clusters of elongate sporangia from Australia (Lang and Cookson, 1935). The genus *Zosterophyllum* has a far greater geographical distribution than in Zone II, being represented by several species (Australia – Lang and Cookson, 1935; Germany–Kräusel and Weyland, 1935; Russia–Ananiev, 1960; ?South Africa–Plumstead, 1977; China–Lee and Tsai, 1978).

The description of *Sawdonia ornata* (Fig. 1N), a zosterophyll with spiny axes from Siegenian sediments of Arctic Canada (Hueber, 1971) marks the earliest appearance of a plant which had a world-wide distribution in the Emsian (see references in Banks, 1975c) and which persisted into the Frasnian (Hueber and Grierson, 1961).

Gosslingia, a zosterophyll characterized by scattered lateral sporangia (Fig. 1H) on smooth axes, has been reported from Wales, Germany and Russia (Edwards, 1970b). The sterile branching system (Fig. 1J) of this plant may be used to illustrate an important general trend in the growth of erect axes. It is described as pseudo-monopodial. one branch of a fork growing more strongly and over-topping the other. Such branching which results in the distribution of a main axis and a number of lateral branches is the commonest type seen in later Emsian floras and is characteristic of the majority of species of the trimerophyte, *Psilophyton*, which first appeared in the Siegenian (see, for example, records of *Dawsonites*, a form genus for isolated trusses of sporangia probably belonging to *Psilophyton*, in Croft and Lang (1942).

A general impression of the growth habit of these early vascular plants may be gained from the extant *Psilotum*, but none of the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pteridophytes I have described so far can be directly related to extant groups (see Bierhorst (1971) and Gensel (1977) for discussion on the relationships between extant Psilotales and early vascular plants). It was in the Siegenian, however, that the lycopods (club-mosses) first appeared. By far the most convincing representative is *Baragwanathia* (Fig. 1L) from Australia (Lang and Cookson, 1935) which has undivided elongate leaves (microphylls), sporangia which appear to be axillary and a characteristically shaped, stellate xylem strand. The excellently preserved *Asteroxylon* in the Rhynie Chert (Kidston and Lang, 1920) is best described as a pre-lycopod as it possesses a level of organization intermediate between zosterophylls and true lycopods. Similarly *Drepanophycus spinaeformis* (Fig. 1M) which first occurred in the Siegenian and extended into the Upper Devonian (Stubblefield and Banks, 1978), has lycopod anatomy and microphylls but lacks the typical axillary sporangia, while *Kaulangiophyton* (Gensel *et al.*, 1969) from the late Lower Devonian has the overall appearance of a lycopod, stalked sporangia but lacks anatomy.

Some of the most important of late Devonian floras are found in north-eastern North America, in the Gaspé, New Brunswick and Maine. Although zosterophylls (e.g. *Crenaticaulis* and *Sawdonia* (Fig. 1D) and rhyniophytes (e.g. *Renalia*) are still present, these floras are

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Fig. 2. (opposite). Late Devonian plants A–J: (A) *Psilophyton princeps* Dawson – sterile axis with blunt spines; Emsian, Canada (× 0·8). (B) *P. forbesii* Andrews – sterile branching axes showing longitudinal ribbing; Emsian, Canada (× 0·5). (C) *P. forbesii* – fertile specimen with cluster of recurved sporangia on lateral branches; Emsian, Canada (× 0·8). (D) *Sawdonia akanthotheca* Gensel *et al.* – loose spike of lateral sporangia terminating spiny axes; ?Emsian, Canada (× 1·8). (E) *P. charientos* Gensel – fertile lateral branch bearing numerous sporangia; Emsian, Canada (× 2·4). (F) *Pertica varia* Granoff *et al.* – fertile specimen with fan-shaped clusters of erect sporangia; Emsian, Canada (× 1·3). (G) *Pertica varia* – sterile pseudomonopodial main axis with dichotomously branching lateral systems; Emsian, Canada (× 0·45). (H) *Chaleuria cirrosa* Andrews *et al.* – erect main axis with spirally arranged lateral branches; ?Emsian, Canada (× 0·7). (J) *P. charientos* – axis with delicate spines; Emsian, Canada (× 2·2).

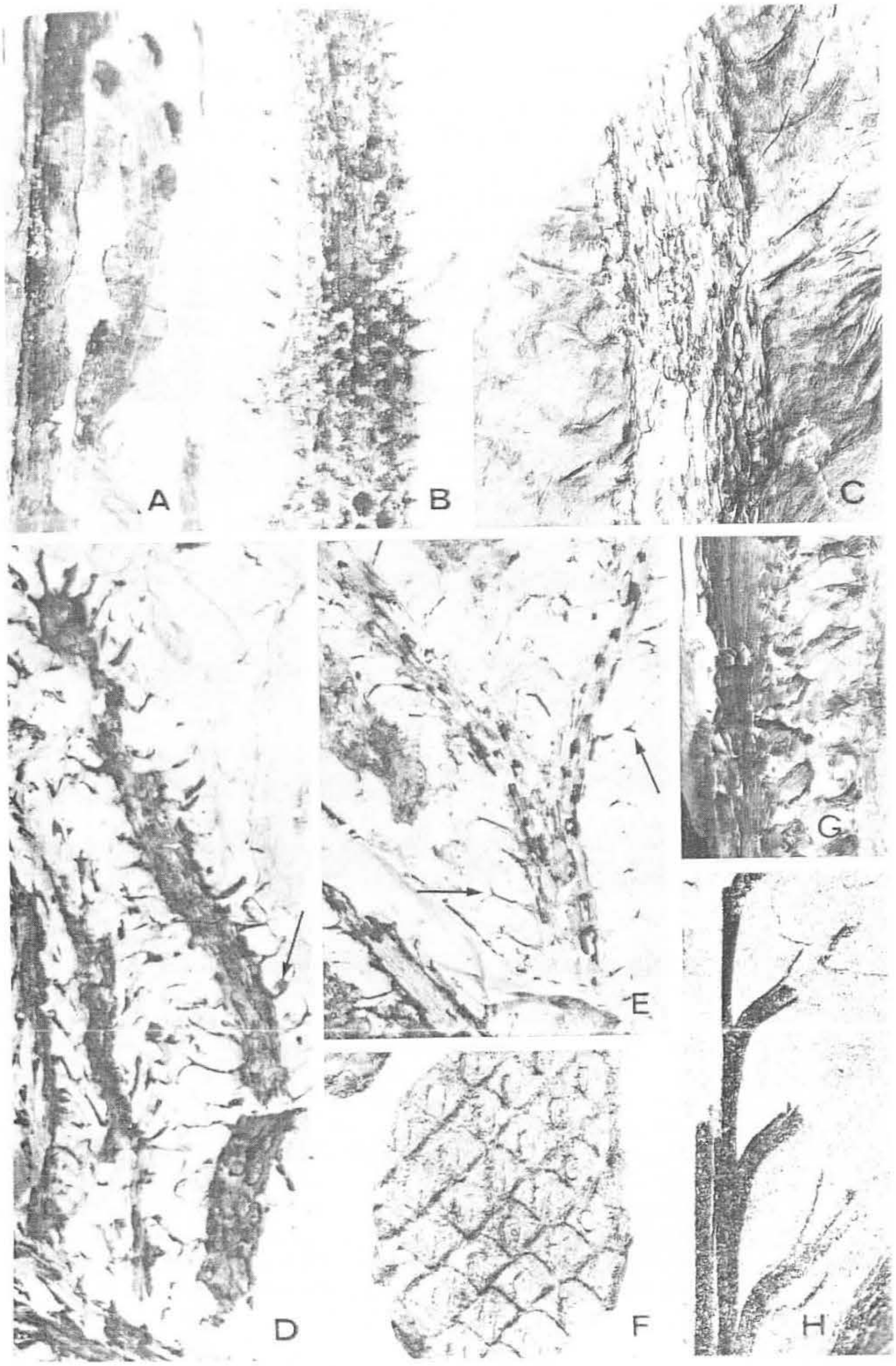
(A) From author's collection; (B,C,E,J) from Gensel, 1979; (D) from Gensel *et al.*, 1975; (F,G) from Granoff *et al.*, 1976; (H) from Andrews *et al.*, 1974.

dominated by Trimerophytina, a group of enormous evolutionary significance in that they are believed to have given rise to the Middle Devonian "fern" complex (Banks, 1980a). *Psilophyton* (Hueber, 1968) is considered to be the most primitive genus in the subdivision (Fig. 2). Six of its seven fertile species are recorded in this area. Branching may be dichotomous, but it more usually pseudomonopodial with lateral branches arranged spirally or distichously. Gensel (1979) suggests that the latter represents an intermediate stage in the evolution of a stem bearing leaves, and that major axes will eventually evolve into stems and the lateral branches into leaves. Some of these lateral branches terminate in trusses of numerous, elongate sporangia (as many as 128 in some species). Surface characteristics of axes are important in delimiting species. *P. dawsonii*, for example, has smooth axes. In *P. forbesii* (Fig. 2B,C) they are heavily ridged. *P. princeps* (Fig. 2A) has truncated peg-like spines, while in *P. charientos* (Fig. 2E,F) spines are pointed.

In *Pertica* (Fig. 2G,H), there is a greater distinction between robust main axes and compacted sterile lateral branch systems; sporangia are organized into spherical masses. Kasper and Andrews

Fig. 3. (opposite) Middle Devonian plants A–H: (A) *Hicklingia edwardii* – spike of lateral sporangia terminating smooth axis (?zosterophyll); Middle Old Red Sandstone, Scotland (× 2·5). Lycopsida B–F: (B) *Archaeosigillaria vanuxemi* (Goeppert) Kidston – stem showing small leaves along the edges and leaf bases on surface near base; Givetian, U.S.A. (× 1·43). (C) *Colpodexylon trifurcutum* Banks – stem showing leaf cushions on surface: long, needle-like leaves are visible at the margin, but do not show trifurcations; Eifelian, U.S.A. (× 1·2). (D) *Leclercqia complexa* Banks *et al.* – stem with some fertile leaves (arrowed): note a single sporangium is borne on the upper surface of a leaf (sporophyll); Givetian, U.S.A. (× 1·6). (E) *L. complexa* – leafy stem with dichotomous branch: in some cases, the two of the five tips of the leaf can be seen (arrowed); (× 1·1). (F) *Bergeria mimerensis* Høeg – part of a small branch with diamond leaf cushions: leafy shoots are called *Protolepidodendropsis pulchra;* Givetian, Spitsbergen (× 0·9). (G) *Duisbergia mirabilis* Kräusel and Weyland – part of a branch with a row of partly covered fan-shaped leaves on right-hand side; Eifelian, Germany (× 0·4). (H) *D. mirabilis* – stem with elongate, partly dissected leaves; Eifelian, Germany (× 0·9).

(A) From Edwards, 1976; (B) from Grierson and Banks, 1963; (C) negative from H. P. Banks; (D,E) from Banks *et al.*, 1972; (F) from Schweitzer, 1965; (G,H) negatives loaned by H. Mustafa.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(1972) consider this increased regularity of branching and higher degree of organization an advance on the condition seen in *Psilophyton* and postulate that the highly branched three-dimensional sterile lateral system may be considered the starting point in the evolution of the fern frond (megaphyll).

A further major evolutionary advance recorded in the later Lower Devonian of New Brunswick is incipient heterospory (Andrews *et al.*, 1974; Banks, in press for dating). All the plants I have described so far have been homosporous; i.e. producers of large numbers of small spores of approximately the same size, their life-cycles presumably similar, at least in outline, to the vast majority of living ferns (Edwards, 1980). *Chaleuria cirrosa* (Fig. 2J) had spores of two sizes which Andrews *et al.* speculate developed into two kinds of free-living gametophytes, a life-cycle intermediate between that of a homosporous pteridophyte and a heterosporous one such as in living *Selaginella*. In the absence of anatomy, the classification of *Chaleuria* presented problems. The authors reached the tentative conclusion that it was a primitive member of the progymnosperms and certainly more highly advanced than the trimerophytes.

3. Assemblage Zone IV : Hyenia *(Eifelian into base of Givetian). Assemblage Zone V :* Svalbardia *(much of Givetian). Figs 3 and 4.*

I propose to consider these together as Banks has indicated that Zone V is characterized by "the abundance and the wide geographic

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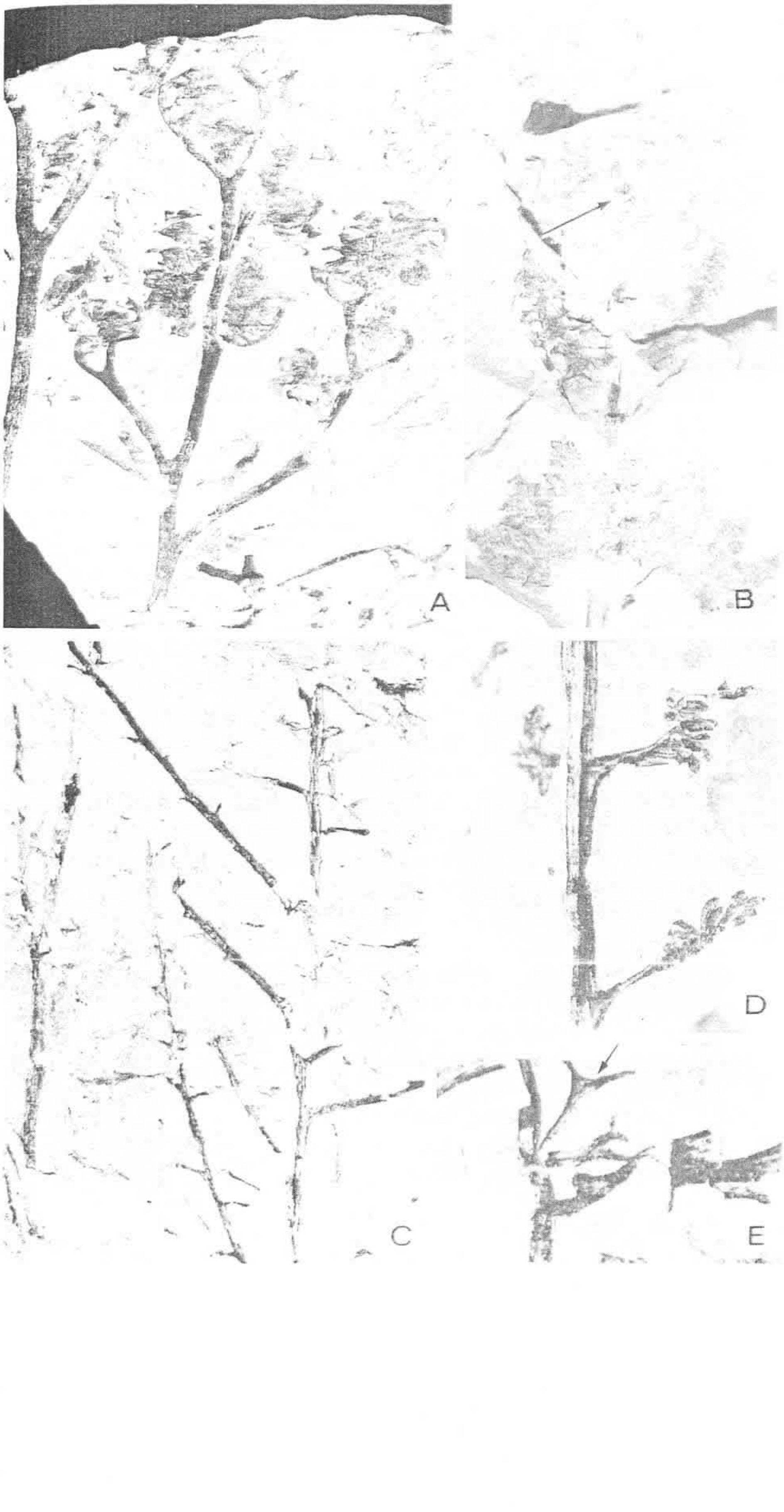
Fig. 4. (opposite). Middle Devonian progymnosperms A–E: (A) *Rellimia thomsonii* Bonamo – the major axes bearing fertile organs with masses of sporangia attached adaxially; Givetian, Belgium (× 0·9). (B) *Tetraxylopteris schmidtii* Beck – fertile specimen in which paired trusses of sporangia are opposite and decussate (arrow indicates region where axis and rock have been removed to reveal sporangia beneath); *n.b.* Frasnian example, U.S.A. (× 0·8). (C) *Aneurophyton germanicum* Kräusel and Weyland – smooth sterile axes showing branching; Eifelian, Germany (× 0·7). (D) *A. germanicum* – fertile specimen showing clusters of elongate sporangia; Eifelian, Germany (× 3·0). (E) *A. germanicum* – dichotomously branching ultimate appendage interpreted as a leaf (arrowed): Eifelian, Germany (× 6·0).

(A) From Leclercq and Bonamo, 1971; (B) from Bonamo and Banks, 1967; (C) from Mustafa, 1975; (D,E) from author's collection.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range of genera that had already appeared in Zone IV" as well as by appearance of more advanced progymnosperms such as *Svalbardia*.

As in the Lower Devonian, it is the lycopods which are most readily identified. Indeed similarities of Lower Devonian representatives such as *Baragwanathia* and the abundance of herbaceous lycopods in the Middle Devonian led to the idea of a relatively unchanged line of herbaceous lycopods from the Devonian to the present day (see, for example, Grierson and Banks, 1963). However, the recent discovery of a ligule in *Leclercqia complexa* (Grierson and Bonamo, 1979), the most intensively studied and best known herbaceous lycopod (Banks *et al.*, 1972; Grierson, 1976) indicates a combination of characters (ligule and homospory) hitherto unknown in the lycopods and not present in modern homosporous *Lycopodium*. Middle Devonian herbaceous lycopods also exhibit a diversity and complexity of leaf morphology not found in recent lycopods, where the leaf is a simple undivided microphyll. *Leclercqia* (Fig. 3D,E) for example, has leaves with five segments; *Colpodexylon trifurcatum* (Fig. 3C) has trifid leaves (Banks, 1944); *Protolepidodendron gilboense* (Grierson and Banks, 1963) has bifurcating leaves, although in species of *Drepanophycus* the leaves are undivided (Grierson and Banks, 1963); and *Archaeosigillaria* (Fig. 3B) has leaves with a pronounced lamina (Fairon-Demaret and Banks, 1978).

Even in the Givetian there are indications that larger lycopods, the stems of which bear the characteristic patterning of later Carboniferous forms, had already evolved. Schweitzer (1965) presents a reconstruction of *Protolepidodendropsis pulchra* (Fig. 3F) from Spitsbergen which had a small trunk approximately 1·5 m high terminating in a sparsely branched crown of leafy axes. Grierson and Banks (1963) report poorly preserved decorticated axes, up to 6·7 cm in diameter from the United States, which they named *Amphidoxodendron*, while from Kazakhstan, Yurina (1968) has described some very well preserved stem petrifactions. Their anatomy is similar to that of Carboniferous lepidodendroids in that an exarch protostele, secondary wood and well-developed bark are all present. Yurina referred these axes to the genus *Lepidodendropsis*, an assignation questioned by Banks (1980b).

Of the two remaining major groups of free-sporing vascular plants, ferns, directly related to and having the appearance of extant forms (i.e. showing the large planated fern frond and abaxial sporangia), did not evolve until the Carboniferous, while the earliest unequivocal sphenopsid is recorded in the Upper Devonian. Middle Devonian representatives are plants consisting of three-dimensional systems of branching axes usually lacking planation or webbing and with sporangia borne on stem-like structures (Scheckler, 1974), In this plexus, however, can be seen the beginnings of more familiar types of organization, e.g. an approach to the whorled arrangement of the leaves of sphenopsids, gymnospermous secondary wood and the anatomy of coenopterid ferns.

Two of the best known Middle Devonian genera, *Rellimia (Protopteridium)* (Fig. 4A) and *Aneurophyton* (Fig. 3C–E), are now considered to be members of the Progymnospermopsida, a class erected for plants with gymnospermous anatomy and pteridophytic (i.e. free-sporing) reproduction (Bonamo, 1975; Beck, 1976). Leclercq and Bonamo (1971) interpret *Rellimia* as a bushy woody shrub in which crowded branches, leaves (the dichotomously branched ultimate appendages) and fertile organs are all borne spirally. These fertile organs are far more highly organized than those of the trimerophytes, the sporangium-bearing system being branched once dichotomously then three to four times pinnately and curved adaxially so that the sporangia (250–400) are inwardly orientated and form overlapping masses (Bonamo, 1977). *Aneurophyton* also has spiral branching (Fig. 4C) but its fructifications are smaller and less branched (Fig. 4D,E). A fertile axis branches just once, with the two arms curving towards each other forming a lyre shape, each arm bearing two rows of sporangia (Serlin and Banks, 1978; Mustafa, 1975). A closely related genus *Tetraxylopteris* (Fig. 4B), first described from the Frasnian of the United States (Beck, 1957; Bonamo and Banks, 1967), has recently been recorded from the Middle Devonian (Givetian) of Germany (Mustafa, 1975). The Upper Devonian representatives have well-preserved secondary phloem, but the earliest recorded occurrence of this tissue is in another progymnosperm, *Triloboxylon hallii* from the Givetian of the United States (Scheckler and Banks, 1971). This plant also produced periderm or cork around the edge of the plant. In living plants periderm is a protective tissue which replaces the outermost layers of stem or root destroyed as a result of extensive secondary production of xylem and phloem.

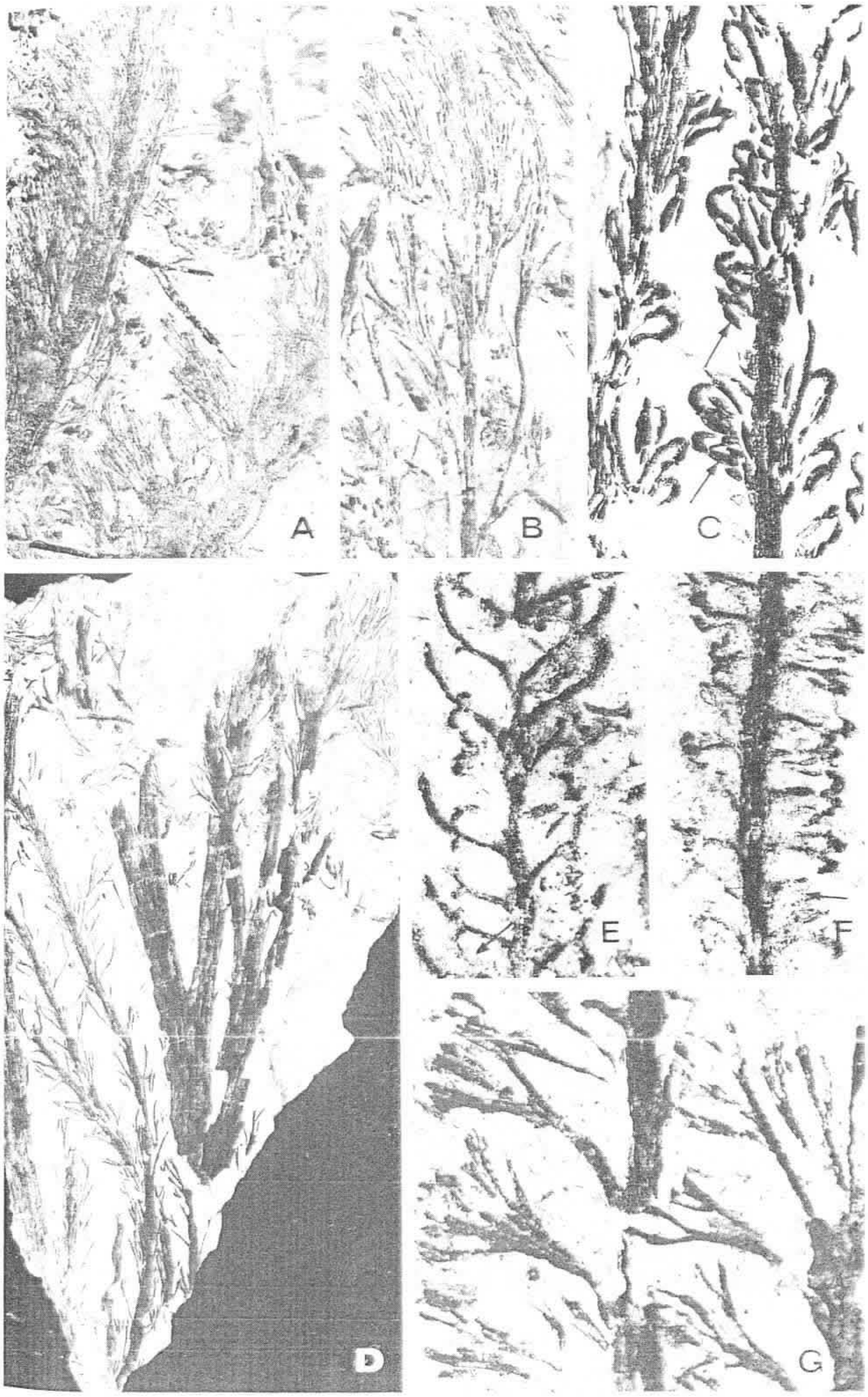
The evolution of a vascular cambium and hence the capacity to increase in girth by the production of large amounts of additional wood (secondary xylem), also increases the potential for growth in height. Although some of the Lower Devonian trimerophytes reached a height of at least 1 m, their axes lacked secondary thickening and rarely exceeded 1 cm in diameter. Andrews *et al.* (1977) suggest that mutual support came from growing in dense stands. The overall size attained by the Middle Devonian progymnosperms is difficult to estimate because of the fragmentary nature of the fossil record, but they are usually interpreted as bushy shrubs or small trees. Calculations based on the casts of the stumps of tree trunks (*Eospermatopteris*) from the Givetian of New York State suggest that trees at least 13 m high evolved by the end of the Middle Devonian.

Chaloner and Sheerin (1979) discuss the wider biological implications of this increase in height with respect both to the development of more complex plant communities displaying ecological "stratification" and to the evolution of heterospory and the seed habit.

The remaining Middle Devonian plants are united in their lack of secondary wood. One of the best known is *Pseudosporochnus* (Leclercq and Banks, 1962; Leclercq and Lele, 1968), a plant estimated to be 2–3m high with a small trunk terminating in a crown of branches. These divide dichotomously and then bear spirally arranged leaves, which divide two to three times in one plane (Fig. 5A,B). The xylem consists of a number of longitudinally running plates and terete strands, anatomy typical of the cladoxylalean ferns.

Fig. 5. (opposite). Middle Devonian plants A–F: (A) *Pseudosporochnus nodosus* Leclercq and Banks – two branches with numerous leaves : note characteristic patterning on stems; Givetian, Belgium (× 0·7). (B) *P. nodosus* – narrower branch bearing several much-divided leaves; Givetian, Belgium (× 2·4). (C) *Calamophyton primaevum* Kräusel and Weyland – fertile axis bearing numerous sporangiophores (examples of sporangia are indicated by arrows); Eifelian, Germany (× 3·0). (D) *C. primaevum* – sterile specimen illustrating branching pattern and forked leaves; Eifelian, Germany (× 1·0). (E) *C. primaevum* – fertile axis: note the well-developed sterile tips of the sporangiophotes, sporangia being borne on the recurved segments (arrowed); Eifelian, Germany (× 2·5). (F) *Hyenia elegans* Kräusel and Weyland – upright fertile axis with sporangiophores: an attached sporangium is arrowed; Eifelian, Germany (× 2·2). (G) *H. elegans* – upright sterile axis bearing dichotomously branching leaves; Eifelian, Germany (× 3·0).

(A,B) From negatives from M. Fairon-Demaret; (C,D) from H. Mustafa; (E) from Schweitzer, 1973; (F,G) from Schweitzer, 1972.


A
B
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Hyenia (Fig. 5E–G), the Zone IV indicator fossil, has long been considered to be a precursor of the sphenopsids. A rhizome up to 2 m long bears erect aerial branches up to 50 cm high. These produce sterile as well as branched stem-like structures bearing recurved sporangia (sporangiophores). These appendages were originally thought to have been borne in whorls, although now the arrangement is considered to have been spiral (Schweitzer, 1972). *Calamophyton* (Fig. 5C,D) has similar fertile and sterile lateral organs, but lacks a rhizome. Following Leclercq and Schweitzer's description of the anatomy of *Calamophyton* as cladoxylalean, the taxonomic status of *Hyenia* as a pre-sphenopsid was questioned (Leclercq and Schweitzer, 1965; Chaloner and Sheerin, 1979). Banks (1968a) however considered that evidence based on reproductive characters should outweigh that from anatomy and retained *Hyenia* in a group called the Protoarticulatae (see also Skog and Banks, 1973).

This is just a glimpse of the kind of problem encountered in discussing the affinities of these Middle Devonian pteridophytes. I have made no attempt to include the numerous compression fossils from the U.S.S.R. (e.g. Petrosian, 1968) or to describe the wide variety of petrified axes from the United States, some of which exhibit anatomy comparable to that of the coenopterid ferns (see Banks, 1968a; Scheckler, 1974).

Finally, although the typical fern frond had not appeared in the Middle Devonian, there are a few records of large, fan-shaped or flabelliform leaves. Some of these were reviewed by Høeg (1942) in his excellent, if somewhat inconclusive, discussion on the systematic position of *Enigmophyton*, an example from the uppermost Givetian of Spitsbergen. Illustrated here is *Duisbergia mirabilis* (Fig. 3G,H) which occurs in the Middle Devonian of Germany (Kräusel and Weyland, 1934). The authors reconstructed the plant as having a tapering trunk up to 3 m high with the top half covered by spirally inserted leaf-like structures and suggested affinity with the lycopods.

SILURO-DEVONIAN LANDSCAPES AND VEGETATION: AN ATTEMPT AT SYNTHESIS

The many difficulties encountered in reconstructing whole plants, in elucidating their affinities, in constructing a plant-based stratigraphy and in deducing their geographical distribution are well documented elsewhere (Banks, 1980b; Chaloner and Sheerin, 1979; Edwards, 1973). Nevertheless we are beginning to reach a better understanding of the composition of Siluro-Devonian floras, of their stratigraphy and their palaeogeography. In bringing together the few pieces of evidence relevant to their ecology, it will become apparent how lamentably little is known about vegetation as a whole, about plant communities and ecosystems.

I shall begin with the one exception. The ?mid-Siegenian Rhynie Chert of Scotland consists of successive layers of peat interbedded with thin layers of silicified sandstone (Kidston and Lang, 1921; Tasch, 1957). The identifiable plant remains in the peat indicate that the peat-formers included species of *Rhynia*, *Asteroxylon*, *Horneophyton* and *Nothia*, but the only plant preserved in growth position is *Rhynia gwynne-vaughanii*. Although it is possible that the plants grew in an environment saturated with siliceous water and therefore formed a specialized and highly adapted type of vegetation, it seems more likely that they grew on a bog which periodically became flooded following the overflow of nearby ponds fed by hot siliceous springs. Tasch believed that the abundance of crustaceans and, to a lesser extent, algae at certain horizons resulted from such episodes of flooding. (The arthropods found in the peat are reviewed by Rolfe, Chapter 6 of this volume). It is considered unlikely that the water-table was permanently high. Kidston and Lang pointed out that stomata occurred near the bases of erect axes, while the abundance of rhizoids on rhizomes suggests that the surface peat was not waterlogged for extensive periods (Rosene and Bartlett, 1950). Whether or not such vegetation was typical of the wetter areas of the intermontane basins of the "Old Red Continent" is impossible to determine. There are fragmentary compression fossils in the more typical Old Red Sandstone sediments below the Chert, but these are unidentifiable.

Scott in his paper on late Palaeozoic vegetation in this volume (Chapter 5) and elsewhere (e.g. Scott, 1977), emphasizes the importance of considering fossil plant assemblages in relation to various lines of sedimentological evidence in the reconstruction of vegetation. In 1973, I made a tentative attempt at this kind of approach in recording the geographical distribution of Devonian floras together with the sedimentary facies in which they are preserved (continental, both external and internal, and marine). Surprisingly (and disappointingly from a palaeoecological viewpoint) many of the floras occur in marine sediments, in both near-shore and deeper water facies. This is the case for all the floras of Pridoli age as well as those in the Ludlow Series, so that the habitats of the earliest vascular plants are highly conjectural (e.g. Edwards, 1980) and also for the extensive floras of the German Lower Devonian. Størmer (1977) discussed the fauna of an Emsian black shale from Alken in the Moselle Valley which was thought to have been deposited in a lagoon. The plants were originally described by Kräusel and Weyland (1935, 1962, 1968) and the reconstruction of a mangrove-type vegetation by Solle (1970) in his sedimentological analysis of the area. Some of the plants (e.g. *Chaetocladus*) were indeed algal and perhaps grew in the shallow waters of the lagoon. There is, however, no direct evidence that the vascular plants were aquatic, as is indicated in reconstructions of *Zosterophyllum rhenanum* and *Protobarinophyton* (Kräusel and Weyland, 1935; Ananiev, 1960) in which only the fertile regions grew above water. A new reconstruction of *Z. rhenanum* (H-J. Schweitzer, personal communication) shows it to have been a terrestrial plant with much-branched rhizomes. It seems more likely that the vascular plants were washed into the lagoon having originally colonized drier coastal areas. Schaarschmidt (1974) has described a putative vascular plant from the same locality, which he interpreted as a halophyte on the basis of swellings at the bases of the main axes and lateral branches. This raises the interesting question as to whether salt-marsh vegetation existed in early Devonian times. Salt-marsh environments today are exceedingly specialized ones, particularly if subaerial exposure is prolonged, and the higher plants (usually angiosperms) which colonize them are highly adapted both anatomically and physiologically to survive periods of severe water stress. Present day pteridophytes are rarely found on salt-marshes although some live in brackish environments and there is no direct evidence for salt-marsh vegetation in the early Devonian (see references in Waisel, 1972; Reimold and Queen, 1974).

Almost all of the plants I have described above grew on "Old Red Land", a landmass which straddled the Equator in Devonian times and which has been the subject of extensive sedimentological, palaeogeographical and palaeoclimatic studies (e.g. Allen *et al.*, 1968; Allen, 1974a; Allen and Friend, 1968; Woodrow *et al.*, 1973). Such studies have provided information on the types of environments available for colonization. Plants are usually considered to have lived along rivers, around lakes or in coastal areas (Andrews *et al.*, 1977; Woodrow *et al.*, 1973; Edwards, 1980). My own research interest is in the Anglo-Welsh area (Allen, 1974a,b; Allen and Tarlo, 1963). In the Brecon Beacons, plant remains are locally abundant in Lower Old Red Sandstone fluviatile desposits, the better preserved ones occurring in grey fine-grained sediments. *Gosslingia*, for example is found throughout a layer several centimetres thick at the Brecon Beacons Quarry (Edwards, 1970b), its axes showing parallel alignment and, on any one bedding plane, with the sporangial zone at the same level on all the axes. Although the alignment itself is produced by currents, the relative positions of the sporangia and the excellent preservation of the plants led me to conclude that they were swept over and rapidly covered with sediment when they were still attached to the ground, and they grew in pure, dense stands near the stream or river and were killed during periods of flooding.

Parallel alignment and vast quantities of axes extending through some thickness of sediment have also been reported from Lower Devonian localities in northern Maine. Andrews *et al.* (1977) interpret the environment as a brackish-water or freshwater coastal swamp, with the plants, e.g. *Psilophyton* sp., growing on drier, slightly elevated (a few metres high) areas usually in monospecific stands, but just occasionally in a mixture of two or three species. *Kaulangiophyton* and *Taeniocrada* are thought to have grown in "small pockets" in the marshland area, possibly occupying quite different ecological niches.

In both these examples plants were growing in areas where the chances of preservation were high and, in the case of the Welsh plants in which anatomy is known, possessed abundant thick-walled tissue which again might have increased the potential for fossilization. This makes it difficult to estimate how representative of the coastal-plain vegetation such preserved plants are. I recently suggested (Edwards, 1980), for example, that plants with predominantly thin-walled tissues such as *Rhynia* would not have been preserved in more typical Old Red Sandstone sediments and that the variety of spores and dispersed cuticular fragments recovered on bulk maceration of sandstones and shales is a further indication of the incompleteness of the macrofossil record.

There were parts of the alluvial flood-plains which were free from sedimentation for long periods, being far away from the influence of rivers (Allen, 1974a), and where conditions for the greater part of the year would probably have been very unhospitable for plant growth. From a comparison of the abundant carbonate units in the Lower Old Red Sandstone of the Anglo-Welsh area with Quaternary soil carbonates (calcretes) of low latitudes, Allen concluded that the climate was warm to hot (mean annual temperature 16°-20°C) and marked by a low seasonal rainfall (100-500 mm). These areas would perhaps have had a surface covering of algae (Edwards *et al.*, 1979) in wetter periods, but it is doubted that such conditions would have been suitable for the growth of higher plants.

There is no direct evidence for upland vegetation in early Devonian times. Comparison of the composition of two Dittonian floras, one preserved in the external (Edwards and Richardson, 1974) and the other in the internal facies of the Old Red Sandstone (Edwards, 1970a, 1975), suggests that by the early Siegenian there was similar vegetation in the intermontane basins and on the coastal plains. It seems not unlikely that plants would have migrated further up the streams into the uplands where the climate might have been more equable. Indeed plants with the type of rhizome system present in *Zosterophyllum* might well have begun to stabilize soils.

Some of the most important research which has resulted in a better understanding of the structure and relationships of Middle Devonian plants has been based on the extensive floras of New York State (e.g. Banks, 1966; Banks *et al.*, 1972; Bonamo, 1977; Matten, 1974, and reference cited therein), but as yet there have been few attempts at palaeoecological analysis even though information is available on the sedimentology, palaeogeography and palaeoclimates (Allen and Friend, 1968; Woodrow *et al.*, 1973) of the Catskill region. Matten (1974) compared the composition of the more-or-less contemporaneous floras from Cairo and Gilboa in New York State. Apart from *Eospermatopteris-Aneurophyton* he found them to be quite different, the former being dominated by ferns and progymnosperms and the latter by lycopods and sphenopsids, which comparison with later Carboniferous floras suggested a swampy environment. In addition, the swollen bases of *Eospermatopteris* trunks appeared to have been preserved *in situ*. Matten concluded that it was perhaps premature to speculate on the detailed ecology of such assemblages, but suggested that their differences in composition indicate that vegetation was not uniform with "populations of different plants growing in different places, forming different communities" (Matten, 1974, p.315).

This review has been concerned with plant macrofossils, but there is also some palynological evidence to support ecological diversity in the Middle and Upper Devonian (Richardson, 1969). In a preliminary comparison of the composition of spore assemblages from a number of depositional environments, Richardson found that assemblages from marine or lower flood-plain-marginal deltaic facies are dominated by the thick-walled spore *Geminospora*, and that *Ancyrospora* with bifurcating spines and the pseudosaccate *Rhabdosporites* are commonest in sediments deposited in fresh water. He speculated that the plants producing *Geminospora* were halophytes either growing on delta swamps or in backswamps or levels in the lower flood-plain, but that the *Rhabdosporites*- and *Ancyrospora*-producing plants colonized the upper flood-plain or nearby freshwater lakes. Recent advances in elucidating the identity of these parent plants are summarized by Allen (1980). *Rhabdosporites* has been isolated from *Tetraxylopteris* (Bonamo and Banks, 1967) and from *Rellimia* (Leclercq and Bonamo, 1971). *Geminospora*-type spores have been found in other progymnosperms such as *Aneurophyton* (Streel, 1964). In similar analyses of Lower and Middle Devonian spore assemblages from Belgium and elsewhere, Streel (1964, 1967) also recognized a correlation between composition of spore assemblage and environment of deposition which led him to propose the existence of several different types of vegetation in the Devonian.

CONCLUSIONS

Although it has been my main concern to provide information on the kinds of vascular plants which colonized the land in late Silurian and early Devonian times, it is a disappointment to have failed to organize such plants into communities and to place these in their habitats with any confidence. There is some evidence to suggest that Lower Devonian communities were simple in composition, often comprising a dense stand of a single species, although the areas covered by such stands and what factors controlled the distribution of individual species remain unknown. In later communities, although usually impossible to identify individual members, it is possible to consider community structure in terms of evolutionary attainment as increasing complexity in morphology and anatomy resulted in changes in growth and reproductive strategies.

We know nothing about the life-span of the earliest vascular plants, but we can postulate that growth in the aerial axes in *Cooksonia*-like plants was strictly [illegible] production of sporangia curtailing any furth[illegible]se in height. (There is the possibility that a rhizome system acted as a perennating organ and continually produced erect axes, but we know nothing about the basal parts of *Cooksonia*.) The pseudomonopodial type of branching seen in some zosterophylls and trimerophytes indicates that the capacity for continued vegetative growth over longer periods and for the production of larger numbers of sporangia had evolved. Such plants did reach heights of over 2 m (e.g. *Pertica varia*), but remained upright by mutual support derived from growing in dense stands. Although these communities would have provided shade and cover for animals, the amount of light for photosynthesis would also have been cut down.

The evolution of a vascular cambium by the Middle Devonian allowed increase in girth, and hence height, and would have resulted in the stratification of communities. The earliest progymnosperms were probably shrubs, but because they lacked planated webbed leaves, there may have been sufficient light reaching the ground to allow the growth of a herbaceous layer of vegetation. By the end of the Middle Devonian there is some evidence that small progymnospermous trees with well-defined trunks had evolved; the arborescent habit also being exhibited by ferns such as *Pseudosporochnus* (with the growth form of a modern tree fern) and by the lycopods, e.g. *Lepidodendropsis* (Yurina, 1969). Chaloner and Sheerin (1979) relate this increase in size of individual plants and the resulting complexity of communities to the evolution of heterospory and the seed habit. In addition this change in reproductive strategy would have permitted the colonization of much drier environments. In the majority of extant homosporous pteridophytes, the gametophyte, an independent plant, requires abundant moisture for both vegetative growth and reproduction (Edwards, 1980). It is therefore restricted to damp, humid environments and, because the sporophyte develops directly on the gametophyte following fertilization, this in turn governs the distribution of the sporophyte. The appearance of heterospory in the early Devonian marked the beginning of the elimination of the independent free-living gametophyte. This level of organization was attained in several lines of pteridophytes, but it is the progymnosperms which are considered to have given rise to the earliest seed plants. The first seed is recorded in the Upper Devonian, the evolutionary climax to a period of extensive diversification in the history of vascular plants.

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